

The Relationship between the Number of Varices and Total Shell Length in Some New Zealand Cymatiidae (Gastropoda : Prosobranchia) and its Ecological Significance

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(1 Plate; 6 Text figures)

MEMBERS OF THE MOLLUSCAN family Cymatiidae exhibit an extreme form of discontinuous growth (LAXTON, 1970). Individuals of a species may grow rapidly, adding half a whorl to their shells in a few weeks, after which shell growth ceases for periods ranging from a month to as long as two or more years. A flared lip or varix, bordering the shell aperture, is laid down at the end of each growth period. These varices are partially buried by succeeding whorls and provide a permanent, visible record of the number of growth stages taken by an animal to produce its shell. Varix production in the cymatiids studied is neither an annual nor seasonal phenomenon, and is in no way indicative of the age of an individual. MACKENZIE (1960) reached the same conclusion regarding varix production in the muricid gastropod *Eupleura caudata*.

For a particular cymatiid species, the distribution of varices on the shell appears to be regular, with the angle between one varix and the next more or less constant. Thus, within a species, shells with the same number of varices may be expected to have approximately the same total length provided the spiral pattern of the shells remains constant throughout growth.

The distribution of varices was examined for 13 species of Recent New Zealand cymatiids. Both inter- and intra-specific variations were examined and an attempt was made to link intra-specific differences to environmental conditions, especially food availability.

MATERIALS AND METHODS

The shells of 13 species of New Zealand cymatiids were examined and the total shell length, number of varices,

the position of the first varix and the angle between successive varices (measured about the protoconch), were recorded for each individual. For each of the common species {*Mayena australasia* (PERRY, 1811), *Monoplex australasiae* PERRY, 1811, *Cabestana spengleri* (PERRY, 1811), *Charonia rubicunda* (PERRY, 1811) and *Ch. capax* FINLAY, 1926} several populations from different habitats were analysed separately.

The rarer species {*Austrosassia parkinsonia* (PERRY, 1811), *Cabestanimorpha exarata* (REEVE, 1844), *Argobuccinum ranelliformis tumidum* (DUNKER, 1802), *Ranella olearium* (LINNAEUS, 1758), *Cymatoma tomlini* POWELL, 1955, *Annaparemma verrucosa* (SOWERBY, 1825), *Cabestana waterhousei segregata* POWELL, 1933, and *Fusitriton laudandum* FINLAY, 1926} were examined from shells in private and museum collections. Supplementary observations were made on live material whenever it became available.

Estimates of the abundance of simple ascidians, upon which some of the commoner species feed, were made by measuring the percentage cover using a 1/10 m² quadrat.

RESULTS

Three distinct growth patterns can be recognised, and these are characterised by *Mayena australasia*, *Cabestana spengleri* and *Monoplex australasiae* (see Plate).

Mayena australasia

In *Mayena australasia* the first varix is formed approximately half a whorl from the protoconch and subsequent

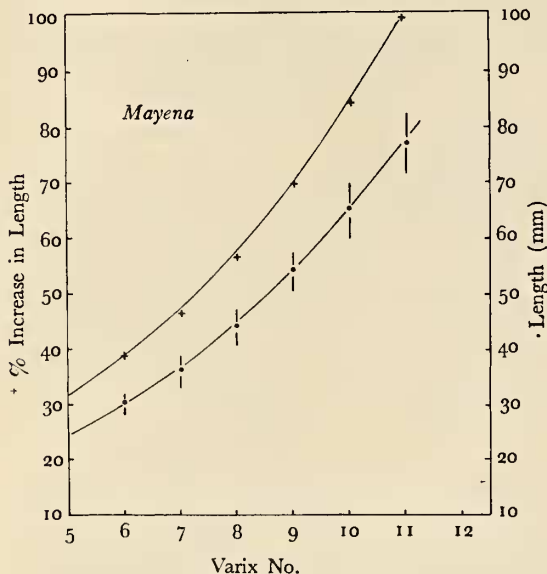


Figure 1

Percentage increase in shell length per varix (+) and mean length and standard deviation (●) plotted for each varix number in *Mayena australasia*

varices are laid down at regular intervals until the adult size is reached. Figure 1 shows the mean shell length and standard deviation for varices 5-12 in the *M. australasia* sampled. Animals with less than 5 varices were not found in sufficient numbers to be included in the analysis. Variations between individuals for each varix number is small, giving a regular increase in length with the addition of each new varix. No significant deviation from this pattern is noticeable when individual populations are analysed, so data have been pooled to give Figure 1. When the angle between each successive varix and the next is plotted as an angle frequency diagram for each varix (Figure 2), the most frequent value is in the region of 180° with a total range of 150° - 240° . Length frequency data plotted on the same diagram for varices 6-10 correspond closely to the shape of the angle frequency histograms for a particular varix. This indicates that the variation in length for each varix is generated by slight differences in the angles between varices, producing slightly longer or shorter shells.

Charonia capax, *Ch. rubicunda*, *Annaparennia verrucosa*, *Austrosassia parkinsonia*, *Argobuccinum ranelliformis tumidum*, *Fusitriton laudandum*, *Ranella olearium* and

Table 1

The relationship between abundance of simple ascidians on the substrate and the ratio of animals with 5 : 4 : 3 : 2 whorls before the first varix, in the population of *Cabestana spengleri*. The ascidian species at Ahipara is unidentified and at the remaining localities *Microcosmus kura* BREWIN is the dominant ascidian.

Area	Locality	Ratio of 5 : 4 : 3 : 2 whorl animals	% of 5 & 4 whorl animals	% cover of ascidians
Exposed West Coast	Ahipara	0 : 43 : 10 : 0	81.1	60 - 70
West Coast Harbour	Mill Bay	3 : 56 : 1 : 0	98.3	50 - 60
	Mill Bay (Fringe)	0 : 0 : 3 : 0	0.0	0.5
East Coast Harbour	Parengarenga (Te Hapua)	3 : 12 : 5 : 0	75.0	40 - 50
Whangarei Heads	McDonald Bank	0 : 13 : 0 : 0	100.0	50 - 60
	McLeod Bay (N)	0 : 29 : 3 : 0	78.3	30 - 40
	McLeod Bay (S)	0 : 7 : 5 : 0	58.3	10
	Taurikura	0 : 10 : 11 : 0	47.6	10
	Reotahi	0 : 2 : 5 : 0	40.0	5 - 10
	Urquhart's Bay	0 : 3 : 10 : 0	23.0	2

The correlation coefficient between the percentage of 5 & 4 whorl animals in the population and the percentage cover of ascidians in the area is 0.98

Cymatoma tomlini are other cymatiid species found in New Zealand waters which exhibit an apparently similar growth pattern.

Cabestana spengleri

In *Cabestana spengleri* there is considerable variation in the position of the first varix. It may be laid down either 2, 3, 4 or 5 whorls from the protoconch.

Populations of *Cabestana spengleri* have been analysed in 3 groups based on broad habitat differences. They are:

- The Mill Bay population - which lives on silty, ascidian covered, low-tidal rocks in the relatively sheltered west coast Manukau Harbour.
- The Ahipara population - which lives intertidally on an exposed rocky shore in the far North (Figure 3).
- A North Island East Coast population - which consists of a number of groups of animals living both intertidally and in shallow water. Animals from the Whangarei Harbour area are not included in this group but were analysed separately (Table 1).

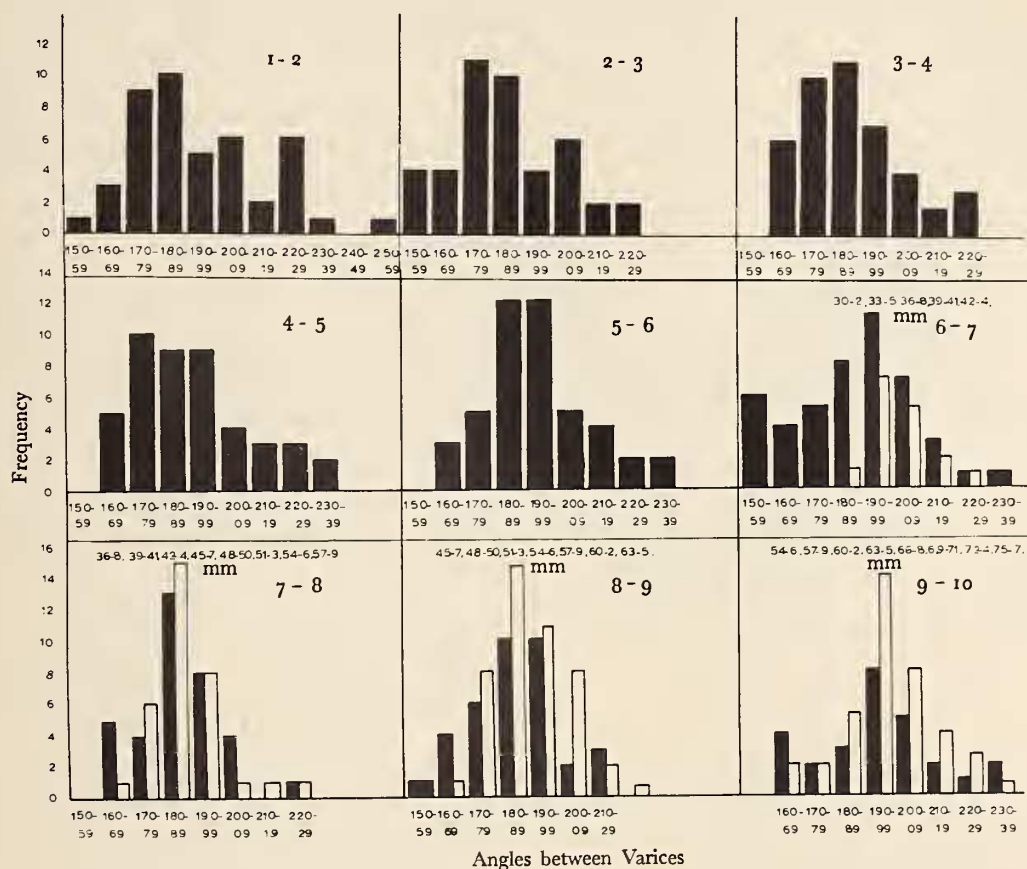


Figure 2

Angle frequency histograms (black blocks) and corresponding length frequency histograms (white blocks - varices 6 - 10) for each varix in *Mayena australasia*

Figure 4 shows the relationship between the varix number and total shell length for the 3 populations. There is little difference between the Mill Bay and Ahipara populations, but considerable variation exists between these and the North Island East Coast population. The percentage increase in length for each varix added (Figure 5), however, is practically the same in both groups, the only difference being the length reached by the juveniles before the first varix is secreted. The reason for there being only 3 varices present on the shells of adult *Cabestana spengleri* from Ahipara (Figure 4) is that sexual maturity is reached at a smaller size than in animals from Mill Bay, due to the limited amount of ascidian food available to support a relatively dense population (LAXTON, 1970a).

Angle frequency data for the first 3 varices of the Mill Bay population and the North Island East Coast popu-

lation (Figure 6) show that the most common angle between one varix and the next lies between 180° and 210° with a total range of 160° to 260°. Length frequency histograms have the same general shape as the angle frequency graphs showing, again, that small differences in the angles between one varix and the next cause the observed variations in shell length for each varix number within a population. Thus, the shell length at which the first varix is laid down in *Cabestana spengleri* determines the final shell length for a given number of varices, since the angle between each two varices is more or less constant.

Since *Cabestana spengleri* grows rapidly without any major interruption until the first varix is secreted, large amounts of food (simple ascidians) must be required to sustain this growth rate. In Table 1, the ratio of animals

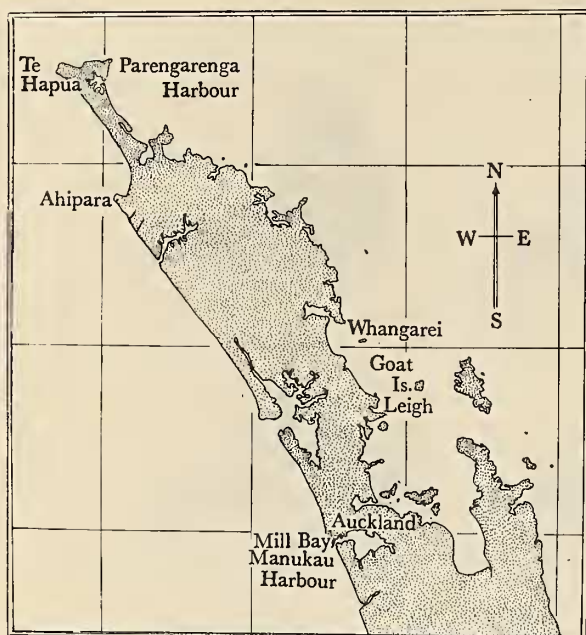


Figure 3

Map of Northland, New Zealand showing the study areas

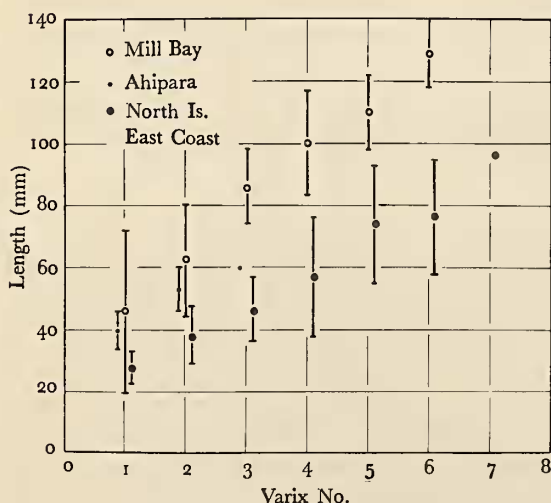


Figure 4

Mean shell length and standard deviation plotted against varix number for 3 populations of *Cabestana spengleri* in Northland, New Zealand

with either 2, 3, 4, or 5 whorls before the first varix and the percentage cover of ascidians on the substrate are shown for several areas in Northland, New Zealand (Figure 3).

Cabestana waterhousei segregata is another New Zealand cymatiid with a growth pattern apparently similar to that of *Cabestana spengleri*.

Monoplex australasiae

The growth pattern of *Monoplex australasiae* is different from that of the other 2 already described. This species is unusual because by the time adult size has been reached only a single labial varix has been formed. Growth is still discontinuous, but instead of a solid calcareous varix being laid down at the end of each growth period, a horny fringe of periostracum is secreted. The distance between fringes is irregular and indicative of the growth rate; short ones indicate a slow rate while longer ones denote rapid growth.

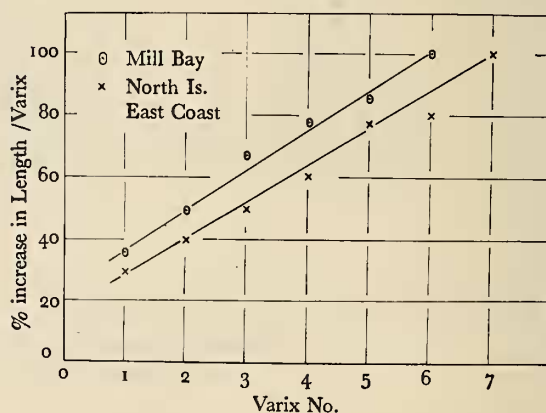


Figure 5

Percentage increase in length per varix plotted against varix number for the Mill Bay and the North Island East Coast populations of *Cabestana spengleri*

The labial varix may be formed 3, 4, 5 or 6 whorls from the protoconch, depending on the amount of available food in the area in which the animal is living. In a small number of older individuals a second varix, added some years after the first, may be present, showing that growth may be resumed under favourable conditions. There is considerable variation in the angle between the first and second varix from animal to animal, unlike both *Cabestana spengleri* and *Mayena australasia*.

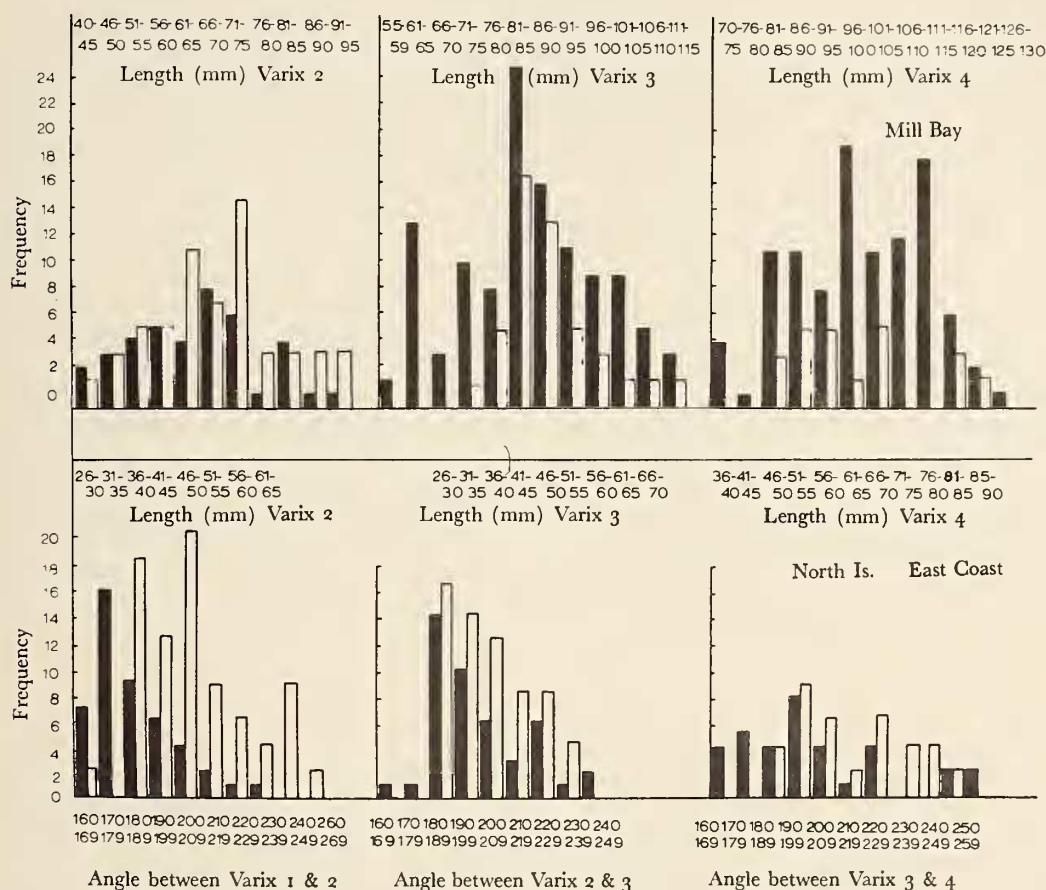


Figure 6

Angle frequency histograms (black blocks) and corresponding length frequency histograms (white blocks) plotted for the first 3 varices of the Mill Bay and North Island East Coast populations of *Cabestana spengleri*

Cabestanomorpha exarata apparently exhibits a similar growth pattern although a second varix is more common.

DISCUSSION

According to HUXLEY (1932), "The majority of animals show unlimited growth; they continue growing, though usually at a constantly diminishing rate, until they die..." Although many molluscs also show indeterminate growth, some families of prosobranch gastropods have determinate growth. Members of the Strombidae and Cypraeidae

(FRANK, 1969) and probably the Struthiolariidae, Cerithiidae, Cassidae and some Volutidae grow continuously until adult size is reached, after which there is no further increase in size. The varix producing families Bursidae, Cymatiidae and Muricidae also exhibit a determinate growth pattern, upon which their system of discontinuous growth has been superimposed.

In the majority of cymatiids studied, growth ceases after a certain size has been reached and this is followed by an adult phase of constant size and long duration.

Three distinct types of growth pattern have been described for the Cymatiidae which impose varying degrees

of restriction on the animals. In the first type, illustrated by *Mayena australasia*, the shell growth pattern is rigorously controlled, providing little opportunity for the animal to adapt to environmental changes. The first varix is laid down close to the protoconch and subsequent varices are formed at approximately half-whorl intervals. This means that *M. australasia* cannot respond readily to an increased food supply by substantially increasing its growth rate, apart from varying the angle of shell added before the next varix is secreted. Some individuals have been observed to grow through nearly twice the normal angle during one growth period while the succeeding angles remained constant. This can be interpreted as a response to increased food supply during that particular phase of growth. The only other way available for *M. australasia* to respond to increased food supply is to add two half-whorls in succession. There is still a delay, however, while the varix is formed and the shell is partially thickened, before shell growth can be resumed.

The shell growth pattern of *Cabestana spengleri* is more flexible and susceptible to environmental influences. The first varix is laid down at varying distances from the protoconch depending on the amount of available food during the early stages of growth. Table 1 shows that the proportion of animals with 5 and 4 whorls before the first varix increases as the percentage cover of simple ascidians, and hence the amount of available food, increases. It is also noticeable that in a heavily populated region like Mill Bay, where the abundance of ascidians is reduced towards the fringes of the area, the ratio of 5:4:3:2 whorled animals changes markedly. There is a greater proportion of 2- and 3-whorled animals towards the periphery of the population. Animals from these fringe areas are responsible for the large standard deviations calculated for the lengths up to the first 2 varices when the population is considered as a whole (Figure 4).

Growth following the laying down of the first varix is subject to the same restrictions as in *Mayena australasia*, with subsequent varices being laid down at half-whorl intervals.

In Foveaux Strait, at the southern tip of New Zealand, *Cabestana spengleri* reaches a very large size. This is due to a slow, rather than rapid initial growth rate. Usually there are only 3 whorls before the first varix. This means

that the shell length by the time the 7th varix is secreted is considerably less than that of a 7-varix northern specimen with 4 or 5 whorls before the varix. Under these circumstances an 8th half-whorl may be added, producing a shell of about 190 mm. It is unlikely that a northern 4- or 5-whorl animal could add an 8th varix because the resulting shell would be in excess of 230 mm. This is some 40 mm greater than the largest *Cabestana spengleri* recorded for the New Zealand region.

A latitudinal or temperature effect could be involved (FRANK, 1969) whereby an animal may grow slowly, but become larger and older near the edge (colder) of its distribution. This implies that the growth rate of *Cabestana spengleri* increases with rising water temperature the further north it occurs, and that growth ceases at a smaller size. While this may be partly true, there are some notable exceptions. For example, in Northern New Zealand, tiny individuals occur with only 2 whorls before the first varix, indicating a slow initial growth rate. These animals are often heavily encrusted and eroded suggesting that they are considerably older than their size indicates. An important feature of the areas in which these small animals live is the paucity of ascidian food. Thus, although temperature may influence the growth rate, it is the abundance of food in the area which permits this rate to be realised.

Further possible evidence that food affects the growth rate comes from the following observation. When a growing *Cabestana spengleri* which had just commenced growing was removed from its food supply, the half-whorl in the process of secretion was completed but no further growth occurred. When the animal was returned to its natural food supply some months later, feeding was intense and within a month a further half-whorl was added to the shell.

Shell growth in *Monoplex australasiae* is subject to none of the morphological restrictions of the preceding two species. Growth may continue as long as there is available food. Whenever a temporary halt in growth occurs, a fringe of periostracum is laid down quickly (complete within two days) and growth may be resumed immediately, if necessary. Even after a calcareous varix has been added to the shell, further unrestricted growth is still possible if conditions permit.

Plate Explanation

Figure 7: Dorsal view of the shells of *Mayena australasia*, *Cabestana spengleri*, and *Monoplex australasiae* illustrating the different types of growth pattern

Figure 8: Aperture views of the same 3 animals (arrows indicate the position of the first varix)

Erratum: On the facing Plate read Figure 7 instead of Figures 1, 2, and 3, and Figure 8, instead of Figures 4, 5, and 6.



Figure 1



Figure 2



Figure 3



Figure 4



Figure 5



Figure 6

